Understory Colonization of *Eucalyptus* Plantations in Hawaii in Relation to Light and Nutrient Levels

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Abstract

Exotic tree plantations may serve as catalysts for native forest regeneration in agriculturally degraded landscapes. In 2001, we evaluated plant species regeneration in the understory of a 7-year-old experimental *Eucalyptus saligna* forest in Hawaii approximately 1 year after the cessation of 5 years of herbicide. These forests were organized in a 2 × 2–factorial design of planting density (1 × 1– or 3 × 3–m spacing) and fertilization (unfertilized control and regular fertilization), which resulted in varying resource availabilities. We found that understory biomass was highest under high light conditions, regardless of fertilization treatment, whereas species richness was lowest under fertilized 1 × 1–m plots. The understory was dominated by species exotic to Hawaii. The most common tree species, the noxious weed *Citharexylum caudatum*, was particularly successful because high light–saturated photosynthe-sis rates and a low light compensation point allowed for high growth and survival under both light conditions. To assess longer-term recruitment patterns, we resurveyed a portion of this site in 2006 and also surveyed five *Eucalyptus* plantations in this region of Hawaii that differed in age (5–23 years), species (*E. saligna, E. grandis, E. cloeziana, E. microcorys*), and management (experimental, industrial, nonindustrial stewardship); all were established on previous agricultural sites within approximately 3 km of native-dominated forest. Again, very few native species were present in any of the stands, indicating that within certain landscapes and for native species with certain life history traits, exotic plantations may be ineffective nursery ecosystems for the regeneration of native species.

Key words: biodiversity, Hawaii, regeneration, secondary succession, tropical forest.

Introduction

An increasingly important question in tropical conservation biology is how to restore native biodiversity, ecosystem function, and ecosystem services to large areas at low costs. Extensive areas of tropical forest have been degraded through harvesting and conversion to non-forest land uses (Houghton 1991; Nepstad et al. 1999), with often devastating impacts on native plant and animal biodiversity (Uhl et al. 1990; Nepstad et al. 1991; Whitmore & Sayer 1992; Lugo et al. 1993; Cabin et al. 2002). The duration, extent, and disturbance frequency of a land use practice will determine recuperation rates for an impacted site (Uhl et al. 1990; Nepstad et al. 1991), and for sites that have been heavily impacted, active restoration in the form of weed control and planting may be required to assure the return of native forest cover. However, replanting native forest species to degraded landscapes for conservation purposes is often prohibitively expensive. Further, seed of native species may be difficult to obtain, expertise to propagate native material may be scarce, and replanted forests may be subject to same land use pressures as the original forest (Lamb et al. 2005).

Forest plantations represent one of the fastest growing forest types in the tropics (Brown et al. 1997), and these forests may serve as potential catalysts for native forest restoration on degraded tropical lands because they also can harbor significant biodiversity in the understory (Lugo 1997; see also accompanying articles in the *Forest Ecology and Management* special issue on the topic). Further, they may represent a low-cost approach to native forest restoration by providing an economic return through harvest of the plantation overstory while ameliorating site conditions for colonizing native species through improved microclimate, the buildup of litter, enhanced nutrient cycling, and the creation of roosting sites (Parrotta et al. 1997). However, the use of forest plantations for restoration of native biodiversity is also associated with uncertainty. Understory composition may vary as a function of overstory species (Guariguata et al. 1995; Powers et al. 1997), land use (Haggar et al. 1997), and age (Keenan et al. 1997). In addition, colonization by exotic species can limit recruitment of native biodiversity.

Light levels are an important factor driving understory species composition and growth in forests, as demonstrated by both canopy manipulations (e.g., thinning; Thomas et al. 1999) and tree fall gap dynamics (Denslow 1987). Light manipulations in plantations may favor high light–demanding species, which may include exotic species with higher photosynthetic rates or more efficient light use

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than native species (Pattison et al. 1998). Altered nutrient supply, whether by fertilization or nitrogen-fixing overstory trees, may also lead to understory colonization by exotic species (Vitousek & Walker 1989; Huenneke et al. 1990; Maron & Connors 1996; Ostertag & Verville 2002; Hughes & Denslow 2005), particularly if exotics are better able to acquire and use additional nutrients through higher nutrient use efficiency and faster growth rates. Finally, in predominantly agricultural or pastoral landscapes, seed sources of native species can be scarce, whereas those of exotic species are abundant. In a reforestation study in Waiakea, Hawaii, where native forest was directly converted to tree plantations of one of three exotic species, approximately one-quarter of all colonizing understory species were exotic (Harrington & Ewel 1997), indicating that understory recruitment in plantations can be subject to strong invasion pressures even when native seed sources are abundant.

In 2001, we evaluated the biomass and species composition of understory plant communities in a 7-year-old experimental forest of *Eucalyptus saligna*, approximately 1 year after cessation of herbicide control of all understory vegetation. Without herbicide control, the understory was quickly colonized by herbaceous and woody species, and we hypothesized that colonization rate would be controlled by light availability and the fertility treatments. Specifically, we examined the following questions: (1) Is colonization of the forest understory dominated by native or non-native species? (2) How do biomass and the richness and composition of the understory relate to understory light environments and the fertility treatments? (3) What physiological characteristics allow the most successful tree species, exotic or native, to be effective colonizers? Complete herbicide control of our forest understory for 6 years preceding our study, intensive sampling of the entire 30 × 30–m area of each forest plot, and proximity of plots to native-dominated forest (2.5 km) provide an important opportunity to examine how resource supply can alter understory colonization of the most widely planted genus in Hawaii and the tropics.

To assess the longer-term effects of our canopy treatments on understory species composition, we resurveyed our plantation site in 2006 (5 years after our first survey of these plots) for native species while quantifying species presence in one representative plot for each combination of tree spacing and nutrition. To also test the generality of our results, in 2006, we surveyed species richness in five other *Eucalyptus* plantations on the Island of Hawaii that were located 0.5–3 km from large tracts of native-dominated forest and that ranged widely with respect to species, stand age, and management of understory weeds and nutrition.

Methods

Site Description and Experimental Design

The study site is characterized by deep volcanic ash soils (Typic Hydrudands) that are considered ideal for agricul-

ture, with most forest in the region being converted to nonforest land uses in the early 1900s. Through most of the twentieth century, sugarcane was cultivated on much of the Hamakua Coast. Following collapse of the sugarcane industry in the 1990s, approximately 10,000 ha of abandoned sugarcane land on the Hamakua Coast were planted to *Eucalyptus grandis* with the goal of producing chips for the pulp and paper market (Little & Skolmen 1989; Giardina et al. 2000). *Eucalyptus*-based forestry has become a long-term land use across the tropics (Brown et al. 1997); as has been shown elsewhere (Parrotta et al. 1997), these stands may serve an important native biodiversity recruitment function.

The first phase of this study (the 2001 survey) was conducted in a 2.5-ha experimental forest of *E. saligna* near Pepe'ekeo on the Hamakua Coast on the island of Hawaii (lat 19°50′28.1″N, long 155°7′28.3″W). The research site is located at 350 m elevation and has a mean annual temperature of 21°C and a mean annual precipitation of 3,600 mm. In 1994, 1 year after cessation of sugarcane agriculture, the site was plowed to disrupt the plow layer and herbicide applied to control regenerating weeds. The site was then planted with 4-month-old, containerized *E. saligna* seedlings, using an experimental design that included a 2 × 3–factorial of spacing (1 × 1– or 3 × 3–m planting density) and fertility (unfertilized control, delayed fertilization, and high fertilization), with three replicates per treatment combination organized into three randomized blocks, for a total of 18 plots. Plots were 30 × 30 m, and ecosystem measurements were made in the central 10 × 10 m (narrow spacing) or 15 × 15 m (wide spacing). Plots receiving no fertilization (control) were initially fertilized once after planting to assure successful plantation establishment. Continuously fertilized plots were fertilized quarterly from October 1994 to November 2000 with 65 kg N/ha, 31 kg P/ha, and 46 kg K/ha and annual applications of 125 kg Ca/ha, 58 kg Mg/ha, and 10 kg micronutrients/ha. The delayed fertilization treatment was treated the same as the control treatment until April 1998, after which this treatment received the same quarterly additions as the high fertilization treatment.

Measurements

This site has been the focus of intensive work on the response of ecosystem C and water cycling to afforestation following 80+ years of sugarcane agriculture, including work on belowground C allocation and cycling (Binkley & Resh 1999; Giardina & Ryan 2002; Giardina et al. 2004), stand water use (Hubbard et al. 2004), canopy physiology (Funk et al. 2003, 2006), and nutrition- and age-related effects on plant primary productivity (Giardina et al. 2003; Ryan et al. 2004). These studies provide a unique dataset with which to evaluate ecosystem controls on understory colonization. We examined the "unfertilized control" and "restore fertility" treatments in these previous studies. We chose the restore fertility treatment over the continuous

fertilization treatment because fertilizer application rate was more similar to that in commercial settings.

Biomass and Species Composition of Initial Understory Recruitment

Plots were initially sampled in 2001 when the plantation was 7 years old. Across each 30 × 30–m plot, all understory plants were identified using nomenclature that follows Wagner et al. (1999). Aboveground parts of each individual were harvested, dried (65°C), and weighed. The only exception was the creeping herb, *Torenia asiatica*, for which we developed a regression equation to relate percent cover to biomass (ln biomass = 1.0274 + 0.04075 × percent cover; $n = 12$; $r^2 = 0.97$, $p < 0.001$). Belowground biomass of understory plants was not feasible to harvest within the scope of this study.

Physiological Ecology of the Tree Species

For the three tree species encountered—*Citharexylum caudatum* (Verbenaceae), *Spathodea campanulata* (Bignoniaceae), and *Rhus sandwicensis* (Anacardiaceae)—we conducted leaf-level physiological measurements in order to understand the biological basis for their growth success. We focused on tree species as they were abundant and trees can influence the functioning of forest canopies and sub-canopies. We acknowledge that woody shrubs (e.g., *Psidium cattleianum*) and even herbaceous species may affect forest function by inhibiting regeneration of canopy species. For each tree species, we developed light response curves for five randomly selected individuals per species across 3 × 3–m control plots, using a LI-6400 IRGA Portable Photosynthesis System (LI-COR, Lincoln, NE, U.S.A.). Net photosynthetic rate (A, assimilation) was measured on newly formed but fully expanded leaves under chamber conditions of 75% relative humidity, 25°C air temperature, and 400 μmol/mol CO_2. Flow rates were variable in order to maintain relative humidity at a fixed level. Light response of net photosynthesis was measured at eight light levels from 0 to 2,000 μmol m^{-2} second^{-1} of photosynthetic photon flux densities. Light levels were decreased in a stepwise fashion, and at each light level, leaves were allowed to equilibrate for approximately 20 minutes before photosynthesis measurements were recorded. Light-saturated (maximum) photosynthetic rates ($A_{mass(max)}$ and $A_{area(max)}$), light saturation point, and light compensation point were estimated for each species based on the mean of the five leaves using Photosyn Assistant (Dundee Scientific, Dundee, U.K.), which determines these parameters by fitting the light response data to a quadratic model function (Prioul & Chartier 1977). The variables are estimated using least squares fitting regression and the Nelder–Mead minimization routine (Nelder & Mead 1965). Specific leaf area (SLA) was estimated by measuring leaf area of sampled leaves in a LI-COR 3100 area meter and dividing area by leaf dry mass. Leaf %N

and %C were determined by grinding leaves in a Wiley mill and analyzing on a Costech ECS 4010 CN Elemental Analyzer (Costech Analytical Technology Inc., Valencia, CA). Instantaneous photosynthetic nutrient use efficiency (PNUE) was calculated as $A_{mass(max)}/N_{mass}$.

Longer-Term Understory Recruitment Patterns

To examine whether short-term (1 year) patterns were matched by longer-term (5 year) patterns, in 2006, we resurveyed four plots of the Pepe'ekeo plantation. Between 2001 and 2006, stands had not been managed for weeds and were not fertilized. We sampled for presence (but not biomass) of native and exotic understory species in a 2 × 15–m strip through one replicate plot (30-m^2 area) for each combination of spacing and nutrition. Although the 2001 and 2006 sampling overlapped, we do not anticipate that the 2001 sampling had a large influence on subsequent understory recruitment patterns, particularly of native species. Because all plants except *Torenia* were removed in 2001, different individuals are compared between 2001 and 2006. Few native species were encountered in 2001, so we anticipate that the removal of an exotic-dominated understory in 2001 would have benefited the recruitment of native species between 2001 and 2006. Critically, in 2006, we found no native species in resurveyed plots, and we encountered very few native species during our native species survey of the entire experimental area (within and between experimental plots).

To further examine whether our findings for an initially intensively managed experimental forest could be generalized to other exotic *Eucalyptus* forests in Hawaii, we also surveyed two 7-year-old industrial plantings of *E. grandis* (at high and low elevations), adjacent 5-year-old nonindustrial plantings of *E. microcorys* (higher leaf area index [LAI]) and *E. cloeziana* (lower LAI), and a 23-year-old experimental planting of *E. saligna*, adjacent to the Pepe'ekeo plots. Again paired intensive (30-m^2 area) and extensive surveys were conducted. These stands were selected because of proximity to large areas of native-dominated forest, because of overstory species and management diversity, and because stand ages vary (5–23 years).

The high-elevation industrial, nonindustrial, and the low-elevation industrial plantings are located upslope of the town of Papa'aloa, approximately 25 km northwest of the Pepe'ekeo plantings, and are 1.0, 1.3, and 3.2 km down slope, respectively, from the base of the Laupahoehoe Natural Area Reserve. The Pepe'ekeo and 23-year-old experimental plantings of *E. saligna* are located approximately 2.5 km down slope from the base of the Hilo Forest Reserve. The Papa'aloa stands were all planted at 2 × 3–m spacing. The industrial stands received fertilization at site preparation and occasional broadcast herbicide for understory weed control in the first few years of stand development. The nonindustrial stands received additions of complete fertilization (N, P, K, and other macro- and micronutrients) twice per year for the first

3 years of stand development and once per year thereafter. Weed control after stand establishment initially included annual mowing, then after year 2 when the canopy closed, spot spraying of aggressive grasses was carried out, primarily *Panicum maximum*. The 23-year-old experimental planting of *E. saligna* was established to examine spacing and nutrition effects on stand growth and so received variable fertilization at planting. Management included little to no-weed control and no fertilization following site preparation (Giardina et al. 2000). For each of these five stands, we randomly selected a starting location from which we established 60-m transects running up slope. We sampled five 2×3–m plots spaced every 15 m along transects for a total area sampled of 30 m^2. In each plot, we noted the species presence and used this to calculate frequency.

Statistical Analyses

The 2001 biomass and species richness data were analyzed using a two-factor analysis of variance (ANOVA), with tree spacing and fertilization as main fixed effects, each with two levels. Biomass values were natural log transformed before analysis to meet the equal variance assumption. Differences between treatment means were determined using orthogonal contrasts. We also correlated these variables to paired plot-level 2-year means (1999–2000) for aboveground net primary productivity, gross primary productivity (GPP), LAI, absorbed photosynthetically active radiation (APAR), leaf net primary productivity, litterfall, soil temperature, and total belowground carbon allocation (TBCA). Details on how these measurements were taken in these stands are found in Giardina et al. (2003). We analyzed all the physiological measurements on the tree species with one-way ANOVA.

Importance values were determined by summing the relative dominance (based on biomass) and relative frequency for each species. Nonmetric multidimensional scaling (NMS) was run on species data (biomass and presence–absence) using Bray–Curtis similarity matrices to see if treatments resulted in distinct groupings. All univariate statistics were done using JMP (SAS Institute 1995), and multivariate statistics were analyzed using Primer 5 (version 5.2.9) (Clarke & Gorley 2001).

Results

Canopy Conditions of the Plantation

Despite large additions of complete fertilizer during earlier studies at Pepe'ekeo, no treatment differences in soil nutrients or soil C were detected after 30 and 66 months of stand development (years 2.5 and 5.5), except for small changes in soil potassium availability (Binkley & Resh 1999; Binkley et al. 2004). The high rainfall environment makes it unlikely that differences appeared between the last fertilization and either the 2001 or the 2006 surveys. Despite the lack of differences, productivity at the site was strongly nutrient limited (Giardina et al. 2003). Fertilization greatly increased GPP over a 3-year period in this forest and shifted allocation of GPP from the belowground to the aboveground productivity and respiration (Giardina et al. 2003, 2004). In line with these findings, an annual average of $<5 \pm 1\%$ ($\bar{X} \pm 1$ SE) of total above-canopy light reached the understory (95% light interception rates) in fertilized, narrowly spaced plots compared with $19 \pm 4\%$ for unfertilized, narrowly spaced plots. For fertilized and unfertilized stands of widely spaced plots, similar annual averages of $28 \pm 3\%$ of total above-canopy light reached the understory (Giardina et al. 2003).

Biomass and Species Composition of Initial Understory Recruitment

In 2001, we identified a total of 28 species in the understory of the 7-year-old plots at Pepe'ekeo, of which 22 were herbaceous (Table 1). Only *Rhus sandwicensis*, a pioneer tree, and *Psilotum nudum*, a whisk fern, were native. The 26 non-native species included roadside weeds and some well-known naturalized species. Of these, *Andropogon virginicus* and *Clidemia hirta* have been designated by the Hawaii Department of Agriculture as noxious weeds in Hawaii (http://plants.usda.gov). Other invasive weeds included *Citharexylum caudatum*, *Paspalum conjugatum*, *Psidium cattleianum*, and *Spathodea campanulata* (Daehler & Carino 2000). Notably, the woody *Citharexylum caudatum* was found in all plots and therefore across a wide range of light availabilities, whereas *Torenia asiatica*, a prostrate crawling herb, dominated plot-level understory biomass across treatments (Table 1).

Total understory biomass was significantly affected by stand spacing ($F_{[1,8]} = 6.15$, $p = 0.04$; Fig. 1), but neither the fertilization treatment ($p = 0.09$) nor the interaction of light and fertilization was significant (Fig. 1). Biomass was negatively correlated with LAI, APAR, and litterfall, confirming the importance of light (Table 2). For species richness, the main effects of light ($F_{[1,8]} = 43.02$, $p < 0.01$) and fertilization ($F_{[1,8]} = 9.76$, $p = 0.01$) were significant (Fig. 1), as was their interaction ($F_{[1,8]} = 43.02$, $p < 0.01$). Species richness was lowest in the fertilized, 1×1–m plots, but fertilization effects were not consistent across spacing. Richness was negatively correlated with APAR, LAI, and all aboveground measures (Table 2).

NMS of the presence–absence data had an acceptable stress value of 0.13 (Clarke 1993; Clarke & Gorley 2001), indicating that plots of the same light and nutrient levels tended to be more similar in species composition (Fig. 2). However, no acceptable NMS solution could be found for the biomass data.

Physiological Ecology of the Tree Species

Leaf-level physiological characteristics varied among the three common tree species. *Spathodea* maintained leaves with the highest SLA (i.e., thinner leaves), N$_{mass}$, and

Table 1. Relative dominance, relative frequency, and importance value of species found in plots after the cessation of weeding.

Species	Life Form	Relative Dominance (%)	Relative Frequency (%)	Importance Value (%)
Desmodium sp.1	H	0.000	0.719	0.720
Andropogon virginicus	H	0.297	0.719	1.017
Centella asiatica	H	0.000	1.439	1.439
Cuphea carthagensis	H	0.001	1.439	1.440
Begonia hirtella	H	0.001	1.439	1.440
Clidemia hirta	S	0.001	1.439	1.440
Cyperus rotundus	H	0.003	1.439	1.442
Solanum americanum	H	0.004	1.439	1.443
Ipomea triloba	V	0.008	1.439	1.447
Psidium cattleianum	S	0.001	2.158	2.160
Ageratum conyzoides	H	0.005	2.158	2.163
Rhyncospora sp. 1	H	0.011	2.158	2.169
Chamaecrista nictitans	H	0.138	2.158	2.297
Lindernia crustacea	H	0.008	2.878	2.886
Colocasia sp. 1	H	0.075	2.878	2.953
Psilotum nudum	H	0.002	3.597	3.600
*Spathodea campanulata**	T	0.039	3.597	3.636
Rhus sandwicensis*	T	0.047	3.597	3.644
Paspalum conjugatum	H	0.106	3.597	3.703
Mimosa pudica	H	0.363	3.597	3.960
Polygala paniculata	H	0.750	4.317	5.066
Spermacose assurgens	H	0.037	5.755	5.792
Oxalis corniculata	H	0.032	6.475	6.507
Crassocephalum crepidoides	H	0.111	6.475	6.586
Colocasia sp. 2	H	0.024	7.914	7.938
Crocosmia × *crocosmiiflora (Tritonia)*	H	0.211	7.914	8.124
*Citharexylum caudatum**	T	0.092	8.633	8.725
Torenia asiatica	H	97.631	8.633	106.264

Relative dominance is proportion of total biomass of each species; relative frequency is the proportion of plots each species was found in; and an importance value is the sum of relative dominance and relative frequency. Native species are shown in bold face. Life forms are herbaceous forbs, grasses, and sedges (H); shrubs or subshrubs (S); vines (V); and trees (T).
*Species on which ecophysiological measurements were made.

$A_{\max(mass)}$ on a mass basis, but PNUE, $A_{\max(area)}$, N_{area}, and light saturation point were also lowest for this species (Table 3). Although not significantly different, *Citharexylum* maintained the lowest and least variable light compensation point (Table 3). The combination of a high $A_{\max}$ but a low light compensation point indicates that *Citharexylum* can maintain a positive carbon balance under shade and high growth rates under high light. Notably, PNUE in this species was twice as high as in *Spathodea* (Table 3). In line with these results, *Citharexylum* occurred in every plot, whereas *Rhus* and *Spathodea* occurred in only five plots, four being 3 × 3–m control plots, which had the lowest LAI and therefore the highest levels of understory light (Table 1).

Longer-Term Understory Recruitment Patterns

Native species were entirely absent from representative plots sampled in 2006, 5 years after our initial surveys (Table 4). Many of the same exotic species were still present while three new exotic species were observed (Table 4). None of the species sampled within plots in 2006 were native, and we identified only scattered *Cibotium glaucum* (a native tree fern) and *R. sandwicensis* individuals outside the main plots.

In our survey of the other *Eucalyptus* plantations, we encountered single individuals of three native species within the plots (Table 5). In the high-elevation industrial plantation, we observed scattered individuals of *R. sandwicensis* outside the plots, whereas in the 23-year-old experimental planting, we observed scattered individuals of *Cibotium glaucum* and scattered patches of the creeping fern *Dicranopteris linearis*.

Discussion

Recruitment of a Native Understory

Numerous studies in tropical plantations varying widely with respect to canopy species and stand age have identified significant understory recruitment of native woody seedlings and saplings (Guariguata et al. 1995; Keenan et al. 1997; Powers et al. 1997; Zanne & Chapman 2001). Mechanisms may include amelioration of microclimate, reduced competition with light-demanding weed species, creation of roosts for fruit-eating animals, and improved soil conditions (Parrotta et al. 1997). Where canopy trees are removed through harvest to release understory trees, these nursery ecosystems may represent a cost-effective
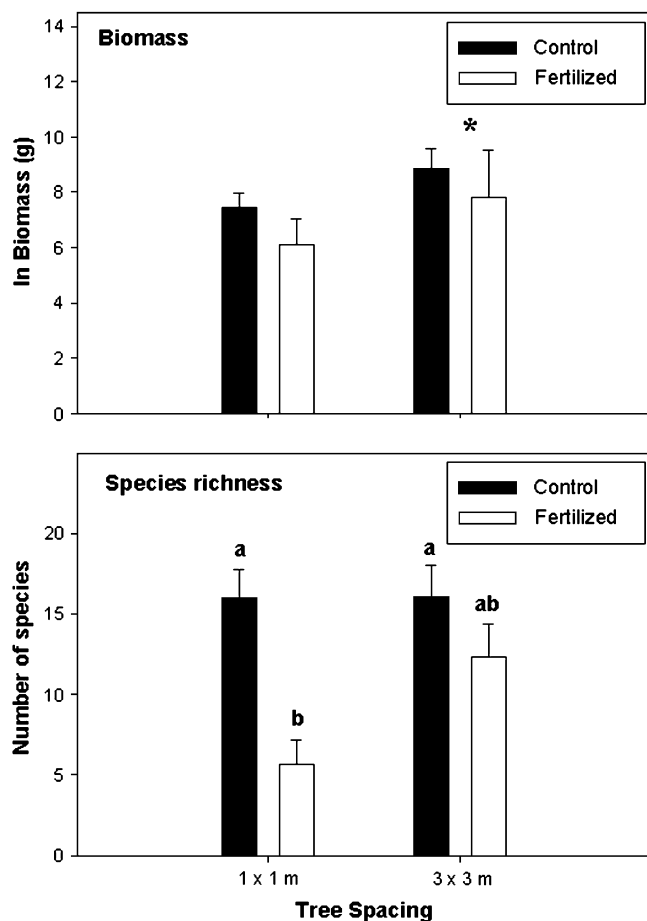
Figure 1. Biomass and species richness ($\bar{X} \pm$ SD) of the understory of *Eucalyptus saligna* plantations at two levels of spacing and nutrient treatment (none or complete fertilizer). Only the light effect was significant for biomass, whereas both effects and their interaction were significant for species richness. Letters indicate significant differences using orthogonal contrasts. For the biomass data, untransformed values are 1,895 ± 792 g; 617 ± 613 g; 8,395 ± 5,954 g; and 6,513 ± 9,711 g ($n = 3$ plots).

way of restoring native forest species to degraded tropical landscapes (Duncan & Chapman 2003).

In 2001, we found significant understory development in 7-year-old *Eucalyptus* forests, but only 2 of 28 species were native to Hawaii. The tiny native whisk fern, *Psilotum nudum*, was insignificant in terms of biomass or abundance. *Rhus sandwicensis* was the only native woody species encountered. This species is a pioneer of disturbed areas (Wagner et al. 1999) and an important component of secondary forests, though not at our Pepe'ekeo site where it was restricted to high-light plots (in 2001). *Rhus* occurred much less frequently in plantation plots in 2006 and across the other *Eucalyptus* sites than the exotic *Citharexylum caudatum*, a tree species that was introduced to Hawaii in 1931 (Wagner et al. 1999), or strawberry guava (*Psidium cattleianum*), which has become very abundant in the understory of native and exotic forests across Hawaii (Hughes & Denslow 2005). Notably, guava had

Table 2. Correlations between plot-level plantation measurements (from Giardina et al. 2003 and Ryan et al. 2004) and the biomass and number of species in the plantation understory.

	Ln Biomass (g)		Species Richness	
	r	*p*	*r*	*p*
Light environment				
APAR (mol/m²/month)	−0.67	0.02	−0.76	0.00
LAI (m² leaf/m² ground)	−0.64	0.03	−0.94	<0.01
Aboveground productivity				
(kg m⁻² yr⁻¹)				
ANPP	n.s.	n.s.	−0.67	0.02
GPP	n.s.	n.s.	−0.67	0.02
Leaf NPP	n.s.	n.s.	−0.69	<0.01
Litterfall	−0.58	0.05	−0.89	<0.01
Belowground productivity				
Soil temperature (°C)	n.s.	n.s.	0.86	0.00
TBCA (kg m⁻² yr⁻¹)	n.s.	n.s.	n.s.	n.s.

ANPP, aboveground net primary productivity; NPP, net primary productivity; n.s., not significant.

a minor presence in our Pepe'ekeo plots but was much more common in the other *Eucalyptus* stands. *Torenia asiatica* was not harvested in 2001, and so frequent occurrence in our 2006 survey is difficult to interpret.

Fertilizer and spacing treatments resulted in significant differences in understory biomass and species richness. The light effect was significant for both biomass and species richness, and this corresponds with the large difference in light transmittance between the two spacings (ranging from 9 to 21% difference; Giardina et al. 2003). A nutrient effect was seen for species richness, which was also correlated to aboveground productivity, with the lowest number of species in the fertilized, 1 × 1–m plots. Fertilization also tended to decrease biomass, although the effect was not significant ($p < 0.09$). Across fertilization treatments, understory biomass and species richness were negatively correlated with the light environment (APAR
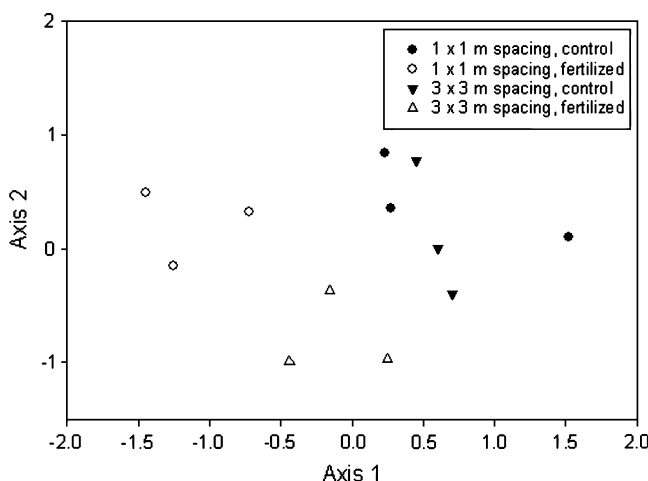

Figure 2. Results of NMS on the presence or absence of species in plots of two light and nutrient levels.

Table 3. Physiological characteristics of the three woody species in the study site.

Species	A_{max} ($\mu mol\ m^{-2}$ $second^{-1}$)	A_{max} ($nmol\ g^{-1}$ $second^{-1}$)	Light Compensation Point ($\mu mol\ m^{-2}$ $second^{-1}$)	Light Saturation Point ($\mu mol\ m^{-2}$ $second^{-1}$)	N_{area} ($g\ N/m^2$)	N_{mass} (%)	C_{mass} (%)	SLA (cm^2/g)	PNUE ($nmol\ CO_2$ $second^{-1}\ mol\ N^{-1}$)
Citharexylum	12.9 ± 2.47[a]	198.8 ± 30.0[a]	4.85 ± 3.20[a]	217.6 ± 48.5[a]	1.03 ± 0.12[a]	1.61 ± 0.34[a]	47.2 ± 0.8[a]	157.4 ± 27.0[a]	118.2 ± 43.4[a]
Rhus	13.7 ± 2.37[a]	236.6 ± 49.1[a]	6.27 ± 6.73[a]	237.4 ± 30.0[a]	0.97 ± 0.06[a]	1.69 ± 0.20[a]	43.2 ± 0.9[b]	173.7 ± 21.8[a]	115.2 ± 27.3[a]
Spathodea	9.7 ± 1.48[b]	345.1 ± 73.8[b]	7.14 ± 4.20[a]	155.0 ± 32.0[b]	0.74 ± 0.08[b]	2.58 ± 0.08[b]	41.4 ± 1.0[c]	354.8 ± 40.6[b]	52.7 ± 8.2[b]

Measurements are maximum photosynthesis on an area and mass basis, light compensation point, light saturation point, nitrogen and carbon concentrations, SLA, and PNUE. The first four variables are derived by curve fitting, and the other four are means and standard deviations. Different superscript letters within a column represent significant differences among species.

Table 4. Frequency of species in 2001 and 2006.

Species	Frequency 2001	Frequency 2006
Chaemacrista nictitans	0.5	0.25
Citharexylum caudatum	1	1
Colocasia sp. 1	0.75	0.75
Colocasia sp. 2	1	1
Commelina diffusa	0	0.25
Crassocephalum crepidoides	1	0.5
Crocosmia × *crocosmiiflora (Tritonia)*	1	0.75
Desmodium sp. 1	0.25	0.5
Mimosa pudica	0.5	0.75
Oxalis corniculata	1	0.25
Paspalum conjugatum	0.75	0.75
Polygala paniculata	0.75	0.75
Psidium cattleianum	0.25	0.75
Psidium guajava	0	0.5
Sacciolepis indica	0	0.25
Spermacose assurgens	1	0.25
Torenia asiatica	1	1

Frequency is the proportion of the four treatments that each species was found inhabiting. In 2001, three plots per treatment were sampled, and in 2006, one plot per treatment was sampled.

and LAI) but not with belowground C allocation (TBCA). These results suggest that understory biomass accumulation is more strongly controlled by light environment, whereas species richness and composition are influenced by multiple factors, including canopy light interception, tree productivity, and fertilization. Belowground allocation does not appear related to understory biomass or composition.

Ordination of the presence–absence data showed that the treatments were distinct, with axis 1 separating fertilization treatments and axis 2 separating the spacing treatments within the fertilized plots. Nutrient supply at our research site had been degraded by 80+ years of sugarcane agriculture, including nutrient export through harvest and erosion. We anticipate that similar results would be obtained on other degraded agricultural sites, which are commonly used for establishing new plantation forests. Plantation tree spacing and nutrition management therefore strongly influence (intentional or otherwise) understory recruitment.

A history of herbicide-based weed control at our site may have resulted in both low diversity and low number of woody species. However, our resurvey of these plots 5 years after initial measurement, during which herbicides were not applied, did not reveal increased diversity of woody species—*Citharexylum, Spathodea*, and *Psidium* were all still the dominant woody species on the site. Notably, the presence of the native *Rhus* species appeared to decline over this same 5-year period. In our survey of other plantations, which varied widely in herbicide use, we found only two native woody species, with *Myrsine* occurring as a single pair of 5-cm-tall individuals.

Our research sites were all within approximately 3 km or less of native protected forest reserves, where there are abundant native seedlings and saplings. However, the low

Table 5. Understory species in a variety of *Eucalyptus* plantations on the Hamakua coast on the Island of Hawaii.

Species	Frequency
Mimosa pudica	0.68
Clidemia hirta	0.60
Sacciolepis indica	0.60
Paspalum conjugatum	0.56
Psidium cattleianum	0.40
Nephrolepis multiflora	0.36
Panicum maximum	0.28
Chaemacrista nictitans	0.24
Schizachyrium condensatum	0.24
Desmodium sp. 1	0.20
Torenia asiatica	0.20
Colocasia sp. 1	0.16
Commelina diffusa	0.16
Crassocephalum crepidoides	0.16
Arundina graminifolia	0.12
Desmodium spp. *(large)*	0.12
Spathodea campanulata	0.12
Cyperus rotundus	0.08
Eucalyptus grandis	0.08
Psidium guajava	0.08
Rhus sandwicensis	0.08
Citharexylum caudatum	0.04
Crocosmia × crocosmiiflora (Tritonia)	0.04
Emilia sonchifolia	0.04
Melastoma candidum	0.04
Myrsine sandwicensis	0.04
Paspalum urvillei	0.04
Pluchea indica	0.04
Pteris cretica	0.04
Unknown sedge	0.04

Native species are shown in bold face. Non-native species are prevalent at all sites. Values are frequency, or proportion of plots, in which a species was present. Data are combined for five sites, with five plots per site.

occurrence of native species in any of the *Eucalyptus* stands suggests that: (1) native propagules are not being dispersed into these plantations due to disperser limitations or due to the life history traits of the native flora; (2) microsite conditions are inappropriate for germination and survival; and/or (3) predators are consuming seeds and/or seedlings.

The Hawaiian archipelago is remote, which meant that natural seed dispersal to these islands was constrained by the seed type, resulting in a disharmonic flora (Carlquist 1966). Hawaii has a number of native families with small bird-dispersed fruits (e.g., Rubiaceae, Solanaceae) but lacks native families with larger fruits that are common in other tropical areas (e.g., Lauraceae, Moraceae, Sapotaceae). The region of this study also has limited number of native frugivore dispersers (P. J. Hart 2007, University of Hawaii at Hilo, personal communication). In fact, *Myrsine sandwicensis* is the only bird-dispersed native plant observed within or near our plots. The remaining native plants are wind dispersed. The dominant canopy tree of Hawaiian wet forests, *Metrosideros polymorpha*, is wind dispersed, and this species has been shown to be limited by safe sites

for germination rather than by dispersal—at least to 250 m of a forest edge (Drake 1992). For this species, we suspect low light levels in conjunction with strong grass competition and distance to seed source limited recruitment (Drake 1993). Successful regeneration of native species also may be limited by seed and/or seedling predation. In Costa Rica, Wijdeven and Kuzee (2000) found that in secondary forests, seed predation decreased seedling abundance of some species by 40%. The impact of exotic seed predators such as rodents and ants, which are abundant across our field sites, on native seedling establishment is poorly quantified in Hawaii.

Our study differs from previous work in *Eucalyptus saligna*, Queensland maple (*Flindersia baryleana*), and Tropical ash (*Fraxinus uhdei*) plantations in Waiakea, Hawaii (850–950 m above sea level), where most understory species were woody and only 25% were non-native (Harrington & Ewel 1997). Contrasting results likely relate to the fact that these Waiakea plantations were established through conversion of native-dominated forest directly to plantations (reforestation) as opposed to a nonforest land use to plantations (afforestation) as was the case for all the *Eucalyptus* stands examined here. Further, the Waiakea plantations were surrounded by native-dominated forest—albeit forest that was somewhat disturbed and that supported some invasive species. In contrast, our study was conducted in a largely agricultural landscape where propagules of native species, either in the seed rain or in the seed bank, were locally scarce.

Physiological Ecology of the Tree Species

The combination of a low light compensation point and a high A_{max} indicates that *Citharexylum* can grow well in both sun and shade and so should be a good plant competitor. In a study of native and invasive rainforest species in Hawaii, *Citharexylum* was shown to grow much faster than native plants under high light conditions (Pattison et al. 1998), but it was also able to maintain relative growth rates under low light (65 μmol m^{-2} second^{-1} maximum) that matched the relative growth rates of native species growing under high light (1,500 μmol m^{-2} second^{-1} maximum). As in our study, Pattison et al. (1998) also reported a low light compensation point. High $A_{area(max)}$, N_{area}, and PNUE but lower SLA (thicker leaves) in this species are indicative that proportionally more nitrogen is allocated to the photosynthetic apparatus than to light-harvesting apparatus (Evans 1989; Reich & Walters 1994). This strategy contrasts that of *Spathodea,* a species less common at our study site but very abundant in gulches in east Hawaii, which appears to have thinner leaves and higher N concentrations but less efficient use of those nutrients. This other invasive, shade-tolerant species had the highest N_{mass} and SLA (thinner leaves) but the lowest $A_{area(max)}$ and PNUE in our study, indicating that relatively more leaf N is directed to light-harvesting proteins that function to maintain photosynthesis at low light levels.

Citharexylum was present in all our Pepe'ekeo plots in 2001 and 2006, as well as other stands, and has aggressively invaded surrounding abandoned sugarcane fields (personal observation). Seed sources for this species were abundant in surrounding abandoned agricultural lands, where the tree can form dense, closed-canopy thickets. We suspect that seed source proximity and dispersal were not limitations. We hypothesize that a long-term study would find rapid spread of *Citharexylum* because it is a shade-tolerant but fast-growing species.

Conclusions

Our study highlights the importance of both local factors such as life history traits of native plants and landscape factors such as fragmentation and distance from intact forest when assessing the potential of plantation overstories to serve as nursery ecosystems for native plant species. On the one hand, distance or connectivity to other forest ecosystems can be quite influential. For example, in a similar tropical study, the most isolated plantation had much lower species richness and stem densities than plantations adjacent to natural forest (Zanne & Chapman 2001), and we suggest that isolation also strongly influenced the lack of native regeneration in this region in Hawaii. On the other hand, in a *Melaleuca* plantation in Oahu, Hawaii, also adjacent to highly disturbed areas, regeneration of the native wind-dispersed tree *Metrosideros polymorpha* was noted (Woodcock et al. 1999), suggesting that dispersal can occur even in isolated forest patches in fragmented landscapes. Further, in large-scale riparian restoration efforts covering 150 km in California, forest isolation was less important in determining native species regeneration than was exotic species presence (Holl & Crone 2004).

There is a critical need to assess whether the understory colonization observed here changes with proximity to intact, native forest edges, where successional communities may contain more native species, such as was the case in New Zealand *Pinus radiata* plantations (Odgen et al. 1997), or whether exotic forests in Hawaii have a low capacity to support native species. Because the aggressive exotic species found in our plots currently are degrading even pristine native forests, we suspect that studies examining limits to biodiversity recruitment in exotic plantations by varying distance to native forest edges will find the latter. The upper industrial plantation was approximately 1 km from native-dominated forest, was relatively unmanaged for approximately 5 years, and yet supported similarly very low recruitment of native species. There is also a strong need for long-term studies. The 23-year-old plantation had the largest number of native individuals, albeit all ferns of which none were in survey plots, perhaps due to the combination of little or no management and more time.

On the Island of Hawaii, as with areas of the tropics that are undergoing urbanization and industrialization (Grau et al. 2003), large-scale agriculture has been replaced primarily by plantation forestry and, on abandoned sites, exotic-dominated successional forests. The resulting "new forests"—mixtures of exotic and native species never before seen together—can have similar species richness and stand structure as native forest stands after six decades of stand development (Lugo & Helmer 2004). How these novel assemblages affect recruitment of native biodiversity remains largely unknown (Hobbs et al. 2006). In Hawaii, as elsewhere (Ewel & Putz 2004), exotic plantations can restore certain ecosystem functions including canopy processes (e.g., light interception) and biogeochemical cycling (e.g., nutrient fluxes through litterfall), as well as having positive effects on the physical environment while providing a buffer to invasive species. With respect to recruitment of native biodiversity, however, our results indicate that exotic plantations are unlikely to facilitate a desired future native biodiversity condition—even after more than two decades of stand development with little management. Instead, these stands appear to largely support the recruitment of non-native plants, many of which are invasive weedy species.

Implications for Practice

- Management of stand density and nutrition can alter understory species richness and biomass. Where native species dominate regeneration, the planting of exotic species that maintain open, low LAI canopies should increase both the diversity and the biomass of native-dominated understory regeneration.
- In windward Hawaii, exotic species are the primary recruits underneath plantations, and exotic dominance appears to persist over time (approximately 23 years), suggesting that long-term utility of exotic *Eucalyptus* plantations for native species recruitment is low.
- Because exotic plantations in this region of Hawaii do not appear to foster recruitment of native biodiversity in the understory, they may not be suitable for passive restoration of native Hawaiian flora. Instead, active restoration methods such as seeding or outplanting may be needed where native seed sources are scarce.
- Species differences between native and non-native species in leaf chemical, structural, and physiological traits can help elucidate mechanisms driving plant distributional patterns. Shade-tolerant exotic species that can maintain a positive C balance under low light conditions should be examined carefully for their invasive potential.

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